



Structural patterns in the mollusc assemblages of *Posidonia oceanica* beds: methodological, edaphic or biogeographical product?

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KEY WORDS: Molluscs, sampling methods, community structure, seagrass, *Posidonia*.

ABSTRACT Mollusc associations living in the *Posidonia oceanica* beds of five geographic areas of the Mediterranean were compared. Complementary sampling methods were adopted: the hand-towed net, more effective on the leaf stratum, and the suction-sampler, more effective on rhizomes. The aim of the study was to gather information on overall coenotic variability, taking into account the contribution of the two main mollusc assemblages stratified along the vertical axes of the plants. Results show a wide variability in the composition of the assemblages, as few species were found to be living in more than one bed. On the basis of the assumptions of the bionomic model of PERES & PICARD (1964), it is very difficult to recognise a unique and well-defined malacological taxocoene for the *Posidonia* beds, which are, in turn, themselves considered as single bionomic units. Present a-ecological data agree better with the 'poly-biocenitic' hypothesis of BIANCHI *et al.* (1989), although b-ecology provides a better understanding of the ecological processes underlying the structural patterns described.

RIASSUNTO Vengono riportati i risultati relativi ad una campagna di campionamento effettuata durante la crociera oceanografica 'MAREVIVO', nell'estate del 1992, a bordo della n/o 'Minerva'. Nell'analisi sono state considerate le stazioni più superficiali (-5m) delle praterie di *Posidonia oceanica* di S. Domino (Isole Tremiti), Gallipoli (Costa Salentina), Lampedusa (Isole Pelagie), Marettimo (Isole Egadi) e Medas (Costa Brava, Spagna). In ciascuna stazione sono state compiute due raccolte: la prima, che campiona circa 20 m² di prateria mediante un retino manovrato a mano; la seconda, effettuata campionando 1 m² di prateria mediante una sorbona manovrata in immersione con A.R.A.

Nei campioni sono stati rinvenuti complessivamente 2122 individui di molluschi, appartenenti a 85 specie (62 di Gasteropodi e 23 di Bivalvi). Di queste solo 34 (40%) sono state campionate con entrambi i metodi, mentre ben 43 (51%) sono state rinvenute esclusivamente nei campioni da sorbona.

I prelievi da sorbona, nonostante la minore area campionata, fanno registrare ricchezze specifiche più elevate, ma presentano valori di abbondanza inferiori rispetto ai campioni di retino. Fra i Gasteropodi, 18 specie sono rappresentate da un solo individuo in un singolo campione. Le famiglie più strettamente legate allo strato foliare (*Trochidae* e *Rissoidae*) sono sempre state raccolte più efficacemente mediante retino. I Bivalvi, invece, sebbene presenti sempre in maniera piuttosto cospicua, sono limitati quasi esclusivamente ai campioni da sorbona.

Si osserva una marcata differenza tra le strutture dei popolamenti delle diverse praterie, ulteriormente sottolineata dall'analisi strutturale, effettuata mediante un modello di ordinamento. Per quanto riguarda l'aspetto qualitativo, solo *Bittium latreillii* è sempre presente in tutti i campioni. *Alvania discors*, *Vitreolina philippi* e *Gibberula philippi* sono comuni a tutti i campioni da sorbona, mentre *Jujubinus striatus* e *Bittium reticulatum* sono presenti in tutte le raccolte effettuate mediante retino.

Tali risultati, se da un lato confermano la diversa efficacia di raccolta degli strumenti utilizzati (il retino per lo strato foliare e la sorbona per il substrato d'impianto e lo strato dei rizomi), dall'altro evidenziano una forte differenza strutturale tra i popolamenti malacologici considerati. Non si registra, infatti, almeno per il taxocene a Molluschi, l'esistenza di una comunità che nel suo complesso possa definirsi 'tipica' del sistema a fanerogame considerato. Ciò suggerisce che vari fattori, tra quali soprattutto la densità dei ciuffi foliari, la natura del substrato d'impianto, e la storia locale delle associazioni malacologiche (piuttosto che la distribuzione biogeografica delle specie), concorrano a determinare le differenze strutturali osservate nei diversi siti.

Quanto rilevato nel presente lavoro sembra essere in contrasto con gli assunti del modello di PERES & PICARD (1964), in cui i sistemi bentonici costituiti dalle praterie di *Posidonia oceanica* del Mediterraneo sono considerati appartenere ad un'unica entità cenotica e bionomica. Il presente studio a-ecologico, invece, sembra meglio supportare l'ipotesi di BIANCHI *et al.* (1989) del 'crocevia ecologico' o della natura 'poli-biocenotica' dei sistemi a *Posidonia oceanica*, che, pertanto, avrebbero caratteristiche strutturali differenti a seconda della storia geologica e biologica dei siti.

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INTRODUCTION

The multifunctional role exerted in the littoral zone by the ecosystem represented by the seagrass *Posidonia oceanica* has, in the last 20 years, prompted a series of investigations. Apart from its widespread and extensive quality (it covers about 2% of the bottoms in the Mediterranean basin), this plant plays an important ecological role as oxygen producer, shelter and nursery site for a rich benthic and necto-benthic littoral fauna. It also provides a stable environment offering opportunities for coevolutionary processes to take place.

The vagile fauna represents one of the most important compo-

nents of this littoral system, both in terms of abundance and species richness. However, the vertical structure of the plant, which increases the habitat complexity and heterogeneity, and the large number of organisms from a variety of taxonomic groups, body sizes and life habits, are all factors which add to the difficulty of collecting this important faunistic component in the most appropriate manner. To overcome this difficulty, different collecting tools and techniques have been proposed and efforts have been made to minimize, or at least standardize, the bias introduced by these different methods (for a review, see RUSSO *et al.*, 1986).

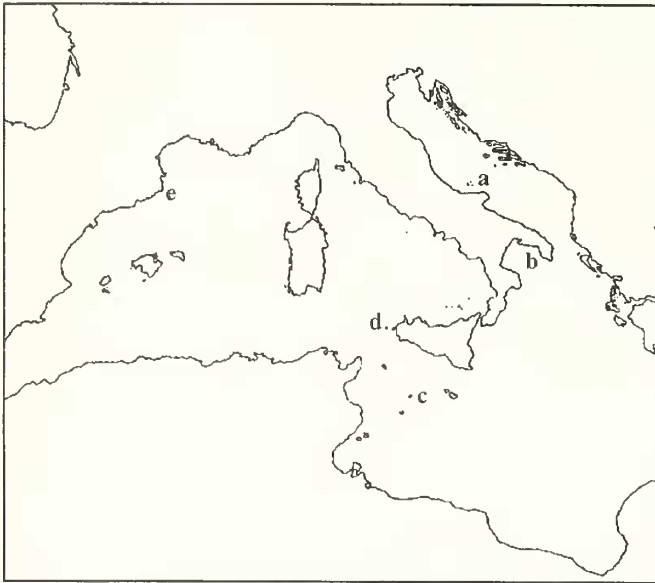


Figure 1. Map with the five sampling sites.

Molluscs are one of the best-represented groups in the vagile fauna of *Posidonia* beds (GAMBI *et al.*, 1992) and have for some time been the object of sinecological studies. The results obtained from recent research indicate a notable structural variability in the malacological community, despite the early studies of LEDOYER (1962, 1966), utilised in the bionomic model of PÉRÈS & PICARD (1964), which recognize a single 'biocoenosis' inhabiting the *Posidonia* beds of the Mediterranean.

The 'intra-site' variability of the mollusc community has been studied both in time, taking into consideration diel and year cycles (RUSSO *et al.*, 1984; 1991 a), and in space, taking into account environmental gradients related to water movement (RUSSO *et al.*, 1983). The 'inter-site' variability is poorly understood, as few comparative analyses on a large geographic scale are available (e.g. RUSSO *et al.*, 1985 a, 1991 b).

This latter aspect seems to be of particular importance in assessing the bionomic 'status' of seagrass systems as, in the most complete study carried out so far, which took into account several *Posidonia* beds of a well defined geographic area (Apulia), BIANCHI *et al.* (1989) found such a high structural variability in the macrobenthic associations as to hypothesize that this system represents a sort of ecologic 'cross-roads', in which four compartments which are 'eco-ethologically' independent of each other are assembled in a 'poli-biocoenotic' complex.

The present paper is the second part of a study comparing a number of mollusc associations from different geographical areas of the Mediterranean. In a previous comparative analysis, a high quali-quantitative variability in the mollusc assemblages was observed (TERLIZZI & RUSSO, 1995). This characteristic of the associations was interpreted as a product of the sampling method utilised, the suction-sampler, which was considered to be effective mainly on the substrate and at the base of the seagrass leaves. This is the most variable portion of the habitat represented by the seagrass (i.e. ranging from rock to mud passing through gravel and sand), the leaf stratum being far more homogeneous in its constitutive components (leaf shoots).

Therefore, the observed coenotic variability may be considered 'topological', being related to 'intrinsic' factors such as the physical characteristics of the sites, rather than to 'extrinsic' ones such as the biological accommodations to large spatio-temporal scales, from which biogeographical and coevolutionary community patterns originate.

The complementary sampling method of the hand-towed net, more effective on the leaf stratum, was considered in the present study and compared with the suction sampler. The aim was to gather more information about both the overall coenotic variability and the contribution made to it by the different strato-coenoses.

MATERIALS AND METHODS

The investigations were part of the oceanographic cruise 'MAREVIVO' (o/s 'Minerva'), in the Adriatic and Ionic Seas and in the western Mediterranean, during summer (July-August)



Figure 2. Collecting methods: (a) suction-sampler (after Russo *et al.*, 1986); (b) hand-towed net (after Russo *et al.*, 1985 b).



1992. Samples were collected at a single depth (~5m), in the *Posidonia oceanica* beds of S. Domino (Tremiti Islands, Adriatic Sea), Gallipoli (Puglia Region, Ionian Sea), Lampedusa (Pelagian Islands, Channel of Sicily), Marettimo (Egadi Islands, Channel of Sicily) and Meda Grande (Medas Islands, Balearic Sea) (Fig. 1).

The density of the prairies was recorded according to the classification of GIRAUD (1977). All the prairies fell into the 'very dense' category (more than 700 shoots/m²), except for that of the Medas, which was classified as 'dense' (500-700 shoots/m²).

For each station two different samples were collected by SCUBA divers. The first sample was collected by an 'air-lift' (or 'suction-sampler') (Fig. 2a) over a surface of one square meter; the second was obtained by a 'hand-towed net' (Fig. 2b), over a surface of about twenty square meters, according to the technique described by LEDOYER (1962) and standardized by RUSSO *et al.* (1985 b).

Molluscs were sorted and identified following SABELLI *et al.* (1990). The descriptive analysis was carried out taking into account the presence of species and their relative and absolute abundances. The comparison of the results obtained by the two collecting methods in the different beds allowed a preliminary evaluation of their efficiency with respect to the different species.

In order to identify coenotic patterns on a large geographical scale, a structural comparison of the malacological associations was performed starting from a matrix of raw data and using the multivariate ordination technique of Correspondence Analysis (CA) (PIELOU, 1984). The significance of the axes was tested according to the method proposed by FRONTIER (1974).

RESULTS

Descriptive analysis

Samples yielded 2122 specimens of Molluscs: 1847 Gastropods (87%) and 275 Bivalves (13%). 907 specimens (43%) were collected by suction sampler, 1215 (57%) by hand-towed net.

With the exception of the Medas, in all other stations the net collected many more individuals than the suction sampler (Fig. 3a). On the contrary, the air lift sampled more species than the net, except from the station of Lampedusa (Fig. 3b).

Overall, 85 species were collected, of which 62 were Gastropods (73%) and 23 Bivalves (27%). 34 species (40%) were collected by both sampling methods, 43 (51%) were exclusively sampled by air-lift and just 8 (9%) exclusively by hand-net.

The number of species yielded by the two sampling tools was quite different in all the stations. In S. Domino, about 50% of species were exclusively collected by net, while in Medas about 70% of species were exclusively collected by suction sampler.

The number of species collected by both sampling tools is quite high in Lampedusa and Marettimo (about 40%), and very low in the other three stations (about 20%). By considering the exclusive and the common species, it is once again evident that in all the stations the suction sampler collected many more species than the net (Fig. 4).

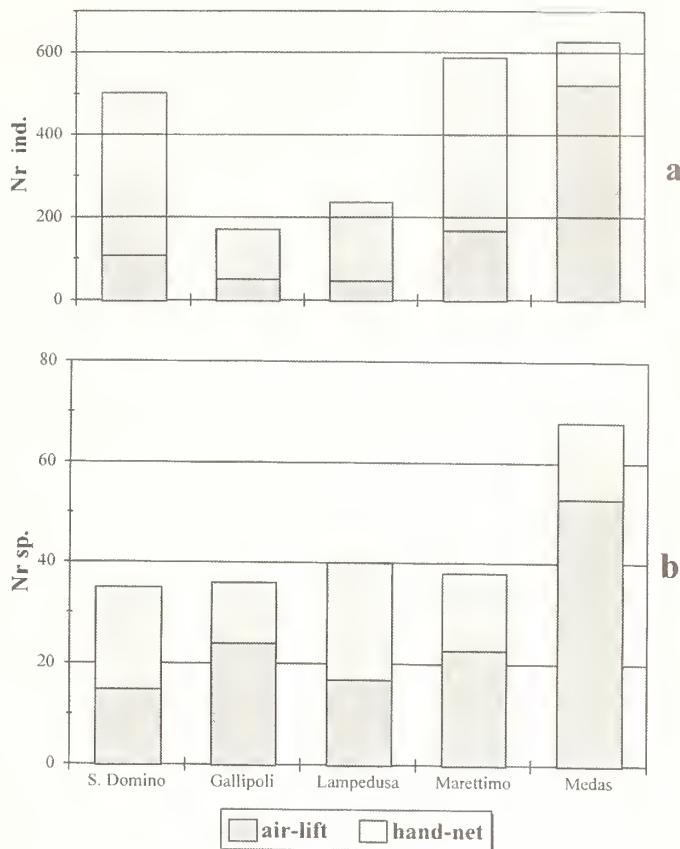


Figure 3. Values of (a) abundance and (b) species richness per sampling method, in the five stations.

As regards the samples collected by air lift, the station of Medas showed the highest values of species richness (53 species, 69%); lower values of qualitative dominance were observed for Gallipoli (31%), Marettimo (30%), Lampedusa (22%) and S. Domino (19%) (Fig. 5a). The highest values of abundance obtained by air-lift were recorded in the station of Medas (523 individuals 58%), the lowest for Gallipoli (6%) and Lampedusa (5%); intermediate values were observed for Marettimo (19%) and S. Domino (12%) (Fig. 5b).

Regarding the samples collected by hand-towed net, the ranking of stations according to species richness has an almost opposite trend: Lampedusa and S. Domino showed the highest values (55 species and 48%), intermediate values were observed for Marettimo (36%) and Medas (36%) while the lowest values were observed in the prairie of Gallipoli (only 12 species, 29%) (Fig. 6a). The highest values of abundance using the hand-towed net were recorded for the prairies of Marettimo and S. Domino (35% and 32%, respectively), while lower values were observed for Lampedusa (15%), Gallipoli (10%) and the Medas (8%) (Fig. 6b).

As regards the distribution of single species in the samples, quite a high number of species (18 species, 21%) were 'singletons' (e.g. present in only one station with a single individual). Only *Bittium latreillii* was present in all the stations and in all

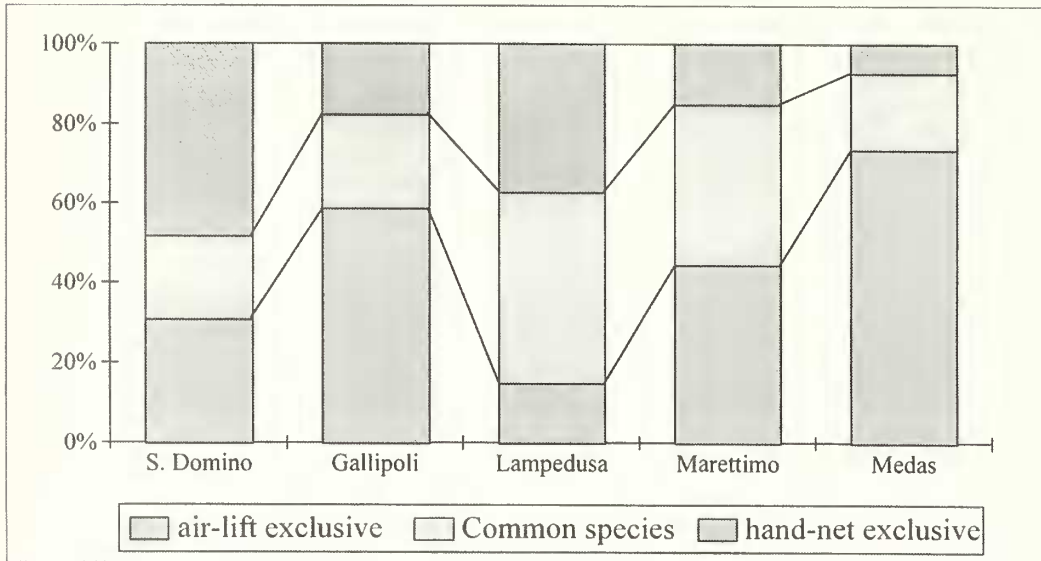


Figure 4. Percent of species collected by both the methods and exclusively by each single method.

the samples, collected by both air lift and hand-towed net. *Alvania discors*, *Vitreolina philippi* and *Gibberula philippii* were present in all air lift samples, while *Jujubinus striatus* and *Bittium reticulatum* were present in all hand-towed net samples. The bivalve species, almost exclusively collected by air lift, were well represented, in quantitative terms, in all the stations and especially in Medas.

Each prairie was well characterised by the high quantitative dominance of particular species: S. Domino by *Rissoella inflata*; Gallipoli by *Bittium reticulatum*, *Bittium latreillii*, *Nassaricus incrassatus*, *Calliostoma conulum*, *Jujubinus striatus* and *Venericardia antiquata*; Lampedusa by *Rissoa auriscalpium*, *Tricolia pullus* and *Alvania lineata*; Marettimo by *Rissoa variabilis*, *Alvania discors* and *Vitreolina philippi* and Medas by *Bittium reticulatum*, *Nassaricus incrassatus*, *Gibberula philippii* and *Musculus costulatus*.

Structural analysis

A first structural analysis was carried out starting from a 82 x 10 matrix (species x (stations x methods)), mathematically treated to obtain a CA ordination model. The model showed, along the first factor, a strong opposition between the samples from the Medas (both hand-net and air lift) and all other samples and, along the second factor, the opposition of the samples of S. Domino to all others (both factors were significant).

A second 54 x 9 matrix (species x samples) was then set up by erasing the samples of the Medas, in order to eliminate distortion in the first factor of the model. In the new CA ordination obtained from this matrix (Fig. 7) the first two factors were significant and showed, along F1, the same pattern present along F2 in the previous model, that is, the opposition of the samples from S. Domino to all others. In addition, some other interesting ordination patterns can be observed in this latter model. Along F1, the two sample points (air-lift and hand-net) of the same site have a saturation which is more similar to that

of other sites; station points have saturations which follow one another consistent with their geographic position: S. Domino and Gallipoli, Lampedusa and Marettimo were ordered respectively, proceeding from the positive to the negative portion of the factor, which could therefore be interpreted as an East-West longitudinal gradient. Along F2, apart from the strong polarisation of the samples collected by air lift at Gallipoli, a clear separation of the samples according to the collecting method was obtained:

all the samples by air lift had positive scores, while all those by hand-towed net were in the negative part of the factor.

DISCUSSION

Remarkable differences in the structure of the mollusc associations living in the five seagrass beds of the Mediterranean were observed. This high structural variability may be interpreted as the result of a number of interacting factors.

First of all, differently-structured malacological assemblages were obtained by the two sampling methods, as clearly shown by the ordination model, in which along F2 the samples by net have an opposite polarisation with respect to those by air-lift.

The material obtained by the two sampling tools was different in both qualitative and quantitative terms. Despite the fact that the hand-net covers a larger sampling area (about 20 m² compared to 1 m²) and collects many more individuals, the suction-sampler gives more complete information on the overall species composition living in a particular prairie stand. Samples collected by air-lift are richer in species and more variable, the apparatus being more effective at the base of the leaves, where the malacological stock is richer in species and reflects the variety of the substrate. Conversely, samples collected by hand-net are less rich in species and less variable, this tool being more effective on the leaves which are inhabited by a more homogeneous malacological stock. Therefore, the suction-sampler would be preferable when the qualitative aspects are to be emphasized with respect to the quantitative ones, as is the case for collections for structural analyses of communities; the hand-net may be more useful when the quantitative aspects prevail over the qualitative ones, as in the case of population analyses.

Secondly, in the large-scale structural comparison of the associations from the five *Posidonia* beds, both sampling methods were effective and gave similar information. This is clearly shown by the AC (F1/F2) ordination model, where the intra-site



sample-points were more closely arranged than the inter-site ones. As a consequence, the hypothesis that the 'inter-site' variability of the malacological associations is the effect of a bias introduced by the sampling method should be excluded. The large-scale variability of the malacofauna of the seagrass beds seems to be so intrinsic to the associations, and the structural 'signal' so strong, that they are recognisable independently of the sampling method utilised. Consequently, the strong structural differences between the Mediterranean sites seem to be related mainly to the edaphic factors characterizing each seagrass bed. The density of the prairie seems to have an important role in determining the strong structural differentiation of the malacological assemblage of the Medas, with respect to all other sites. In this site, in fact, the air-lift was far more efficient than the hand-net, as indicated by the high presence of molluscs more strictly related to the substrate, such as bivalves and, among gastropods, the families of Alvaniiidae and Marginellidae. Apart from the vegetal cover of the substrate (e.g. density of plant shoots), the quality of the substrate itself, its exposure to water movements and the related sedimentation rates may be among the main edaphic factors affecting the quali-quantitative composition of the malacological associations and determining the variety of functional adaptation. In fact, the dominance of herbivore-deposit feeders (e.g. *Bittium* spp.) is typical of seagrasses under conditions of low environmental energy, while, on the contrary, brusher-herbivores (e.g. *Jujubinus* spp. and *Tricolia* spp.), are abundant in conditions of high water movement.

In addition, the information collected suggests the presence of a latitudinal coenotic gradient. This is fairly evident in the ordination model, where the station points show saturation along F1 consistent with their geographical (i.e. longitudinal) positions. There are no species with narrow biogeographical distributions affecting the composition of the assemblages. Therefore, this latitudinal pattern is likely to be of the structural type, a product of the way widely distributed species are sorted together, rather than the result of the presence of endemic species in a narrow region of the Mediterranean. This geograph-

ical aspect is of particular interest and may be a promising field of investigation. In fact, up to now most malacological research activity has focused on investigating the historical aspects of single species, such as their evolution and biogeography, with little or no attention paid to the study of the history of assemblages they form.

Last, but not least, the large variability in the composition of the assemblages described in the present paper implies a great difficulty in recognising a unique and well-defined malacological taxocoene for the *Posidonia* beds. Species co-occurring in the different beds constitute a very low percentage of the total.

Therefore, the present analysis of one of the main faunistic components of the vagile fauna does not agree with the model of PÉRÈS & PICARD (1964), where the Mediterranean *Posidonia* beds are considered as a single biocoenotic and bionomic unit (HP). Present a-ecological data agree better with the 'poly-biocoenotic' hypothesis (BIANCHI *et al.*, 1989), although b-ecology needs to be focused in the future in order to gain a better understanding of the ecological processes underlying the structural patterns described.

CONCLUSIONS

- The suction-sampler and the hand-towed net discriminate the *intra*-site variability, as they sample different parts of the habitat produced by the seagrass. This gives rise to 'method-dependent' patterns which correspond to a real 'topological' stratification of the malacological association within the seagrasses. Therefore, the study of this type of variability needs sampling by both the above complementary techniques.

- When *inter*-site comparisons are performed, a new and stronger structural variability is added, against which the discriminating power of the two methods becomes ineffective, as they produce similar patterns. This new variability may be considered as 'edaphic', being related to local factors affecting the seagrasses. Consequently, for the study of this second type of variability, one of the two techniques may be adopted indifferently.

- A longitudinal trend was observed even if no species with narrow biogeographical distributions were recorded. Therefore this pattern is more likely to be related to the 'history' of the assemblage (e.g. successional stages) rather than to the history of some of the species belonging to them (e.g. evolutionary ecology).

- The high variability in the composition of the malacological assemblages does not fit with the model by Pérès and Picard which considers the Mediterranean systems of *Posidonia oceanica* beds as belonging to a single bionomic unit; on the contrary, our findings represent additional evidence in support of the hypothesis considering the system as an 'ecological cross-roads'.

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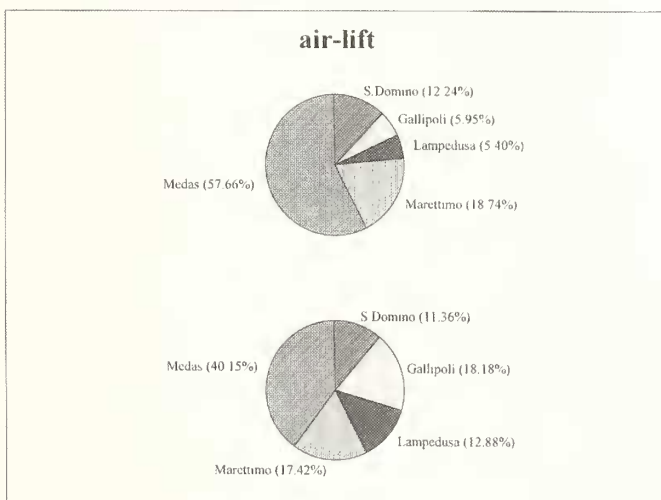


Figure 5. Samples by air-lift: (a) qualitative and (b) quantitative dominances among the sites.

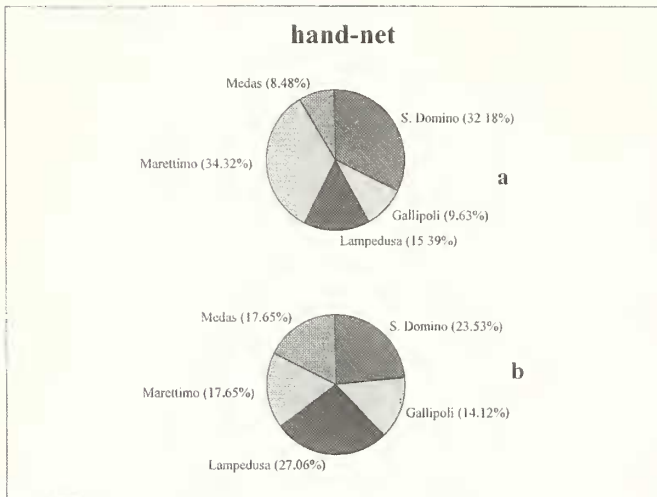


Figure 6. Samples by hand-net: (a) qualitative and (b) quantitative dominances among the sites.

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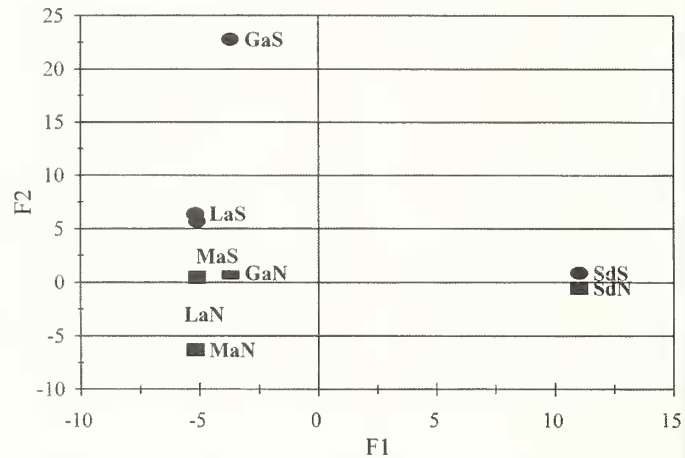


Figure 7. CA ordination model (F1-F2) of sample-points, obtained after the elimination of the peculiar samples of Medas (LaS= Lampedusa, Suction-sampler; LaN= Lampedusa, hand-Net; GaS= Gallipoli, Suction-sampler; GaN= Gallipoli, hand-Net; etc.).